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THE EFFECT OF HOST SIZE UPON THE SEX RATIO OF HYMENOPTEROUS PARASITES AND ITS RELATION TO METHODS OF REARING AND COLONIZATION

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It has often been assumed that the sex ratio is an approximately constant factor for any given insect species under field or laboratory conditions, and figures quoted for this relationship are usually based upon rearings of field samples of varying size, and collected, in most cases, at times of numerical abundance. The sex ratio of a species is in reality exceedingly variable and fluctuations may be due to a number of causes. It is proposed to discuss here some of the factors which bring about these changes, particularly among the parasitic Hymenoptera, and to discuss their bearing upon biological control work.

In general it may be stated that, in the parasitic Hymenoptera, either an approximately equal representation of the sexes or a preponderance of females is the normal condition in nature. Often there is a marked preponderance of females, extending in some instances to the occurrence of only an occasional male among thousands of females, and finally to those species in which reproduction is entirely thelyotokous. Exceptions to the numerical dominance of the females may be noted, as in the case of *Opius melleus* Gehan (Lathrop and Newton, 1933), which showed 37.68 per cent females among 4,962 adults reared from field-collected

Rhagoletis pomonella Walsh over a period of three years. Pemberton and Willard (1918) record only 37.6 per cent females among 26,975 adults of *Opius tryoni* (Cam.) reared from field-collected puparia of the Mediterranean fruit fly (*Ceratitis capitata* Wied.) during two seasons.

The sex ratio is often a rapidly changing figure for a species during the season. *Microterys clauseni* Comp., a gregarious internal parasite of *Ceroplastes floridensis* Comst., in Japan showed the females of the overwintering generation predominating 3 : 1, whereas in the following generation, emerging in June, the ratio increased to 9 : 1. Even more striking is the variation shown to occur in *Tiphia popilliavora* Roh. (Brunson, 1934), a solitary external parasite of the larvæ of the Japanese beetle (*Popillia japonica* Newm.). In this instance the ratio of the adults developing from eggs laid during August was 1 : 2.8, the males predominating, whereas among those from eggs laid during September and later the females predominated 1.5 : 1.

One of the important factors influencing the sex ratio is the size of the individual hosts in or upon which the parasites develop. Attention was called to this fact by Chewyreuv (1913), who found that the great majority of *Pimpla* spp. from large cocoons were females, whereas those from small cocoons were predominantly males. The large-sized hosts of *Pimpla* spp. (mainly *instigator* F.) are of the lepidopterous genera *Sphinx, Saturnia,* and *Gastropacha,* and the smaller species are of *Pieris, Panolis,* and *Bupalus.* Field-collected pupæ of the larger species yielded a large majority of *Pimpla* of the female sex, while the small pupæ produced mainly males. Laboratory tests verified these findings, large host pupæ yielding 100 per cent of female parasites and the small ones 80 per cent of males.

Exenterus sp. from *Lophyrus* cocoons yielded 79 per cent of females from large host cocoons and 47 per cent from the small cocoons, while the corresponding figures for *Campoplex* were 70 per cent and 26 per cent, respectively. In the case of this host the male cocoons are approximately half the size of those of the females.

Chewyreuv attributed the marked disparity in the sex ratio of *Pimpla* to selective oviposition by the parent female. According

to this hypothesis the female is able to deposit fertilized or unfertilized eggs at will, and those destined to produce females are placed in the larger hosts, which provide a greater food supply for the progeny. This explanation of a very interesting phenomenon has been questioned by several authors and a direct nutritional basis offered instead. Others suggest that mated females are attracted to the larger hosts and unmated females to the smaller ones. It is quite possible that a single explanation will not suffice for all cases of fluctuating sex ratio arising from differences in size of the host individuals. At this time, however, we are not concerned so much with the causes which bring about this condition as with the application of the knowledge of these facts to the practices of biological control.

Further information regarding the sex ratio in the Ichneumonidæ is available in the literature. Seyrig (1935) discusses *Pimpla maculiscaposa* Srg. and *Echthromorpha hyalina* Sauss. Both of these species have many lepidopterous hosts and the pupæ of the largest species are approximately 20 times as large as those of the smallest species. The largest pupæ yielded almost exclusively females, whereas from the smallest hosts the males predominate in the ratio of about five to one.

In the case of *Exeristes roborator* F., a solitary parasite of the larva of the European corn borer (*Pyrausta nubilalis* Hbn.), W. A. Baker advises me that insectary rearing on this host at the Toledo, Ohio, laboratory during 1924–27, representing 100,000 individuals, gave a sex ratio of 1 : 1.13, the males predominating. This ratio varied from 1 : 1.63 to 2.45 : 1 in different years and there was considerable variation during the course of each year. Fox (1927) states that in Canada the ratio for insectary-reared material of this species was 1 : 2, the males predominating, and that difficulty was experienced in maintaining a satisfactory production of females. More recently this parasite has been reared upon the pink bollworm (*Pectinophora gossypiella* Saund.) at the Presidio, Tex., laboratory. According to unpublished reports by L. W. Noble, reproduction upon this host, which is smaller than the European corn borer larva, resulted in a sex ratio of the progeny of 1 : 8.5, the males predominating. Emergence of material which developed in the field revealed a ratio of 1 : 4.1. The

possibility of securing a higher production of females by the use of a larger host was investigated and the southwestern corn borer (*Diatraea grandiosella* Dyar) was utilized for this purpose. This change to a larger host was reflected in the sex of the progeny, and resulted in the more favorable ratio of approximately 1 : 2.

In *Calliephialtes messor* (Grav.), a solitary external parasite of the larva of the codling moth (*Carpocapsa pomonella* L.), Cushman (1913) records the females as being in the minority to the extent of 1 : 3 among 528 progeny reared from mated females under insectary conditions. The overwintering brood showed a ratio of 1 : 2.5, and this declined in the third following generation to 1 : 8.8.

The above decline in the proportion of females, when reared in the laboratory, has been duplicated with many species imported from abroad. A striking instance is cited by Bradley and Burgess (1934) in the case of *Cremastus flavoorbitalis* (Cam.), a solitary internal parasite of the larva of the European corn borer in the Orient. The field-collected material which was imported showed the number of females to exceed that of the males by 1.6 : 1. In contrast to this, the results of rearing under insectary conditions, with apparently mated females, practically reversed the ratio, the females being in the minority in the ratio of 1 : 2.2.

Among the Braconidæ some striking figures have been presented by Holdaway and Smith (1932) for *Alysia manducator* Panz., a solitary parasite in the puparia of blowflies in Europe. The hosts studied were *Calliphora vomitoria* L., *Sarcophaga* spp., *Calliphora erythrocephala* Meig., and *Lucilia sericata* Meig., given in the order of relative size. The largest *C. vomitoria* puparia produced females only and the smallest *L. sericata* males only. The proportion of females increased in simple proportion to the increase in size of puparia. This held true within each species as well as between different species. In the larger puparia of *L. sericata* the sex ratio of the parasite was 1 : 1.3, the males predominating, whereas from the smaller puparia the ratio was 1 : 5.1. From puparia of *Sarcophaga* spp. the ratio was 2.1 : 1.

Another solitary parasite of blowfly puparia is *Brachymeria fonscolombei* (Dufour), which has been studied by Roberts (1933). Very extensive rearings were made during 1930–32 and

the sex ratio of all emergences was 1.3 : 1, the females predominating. It is noteworthy, however, that one rearing revealed a female preponderance of 3.5 : 1, whereas another showed a deficiency of 1 : 2.3. It would appear probable that this difference was due to the different numerical abundance of host species, which in turn vary greatly in size, in the respective trap jars.

In the Trichogrammatidæ, represented by *Trichogramma evanescens* Westw., we find the sex ratio responding markedly to a shortage of food resulting from superparasitism. Salt (1936) has shown that where a single female is confined with a given number of host eggs 77.6 per cent of the progeny which emerge are females. Further similar tests, increasing the number of parent females but retaining the same number of available host eggs, revealed a consistent decrease in the proportion of female progeny. The extreme superparasitization induced by confining 50 parent females with 100 eggs yielded only 43.8 per cent female progeny.

Flanders (1935) points out that *T. evanescens* showed females predominating to the extent of 2 : 1 when developing in the eggs of *Estigmene acraea* (Drury). These eggs are sufficiently large to permit a maximum of 10 individuals to complete development in each. At least three *Trichogramma* eggs may be deposited at one insertion of the ovipositor and these normally produce two female and one male progeny. If only a single egg is laid the progeny is invariably female. Large females may be over five times as prolific as smaller individuals. This difference in size may result in the individual females selecting different hosts, as the smaller females are unable to penetrate as thick-shelled eggs as are the larger individuals.

Taylor (1937) has presented evidence regarding two chalcidoid parasites of coconut leaf-mining beetles of the genus Promecotheca, and shows a marked change in the sex ratio in relation to size of host. In *Pleurotropis parvulus* Ferr., from first-instar host larvæ only, the females predominated in the ratio of 1.66 : 1.00, whereas on third-instar hosts the preponderance of females increased to 4.34 : 1.00. A similar situation was found to exist with respect to *Elasmus hispidarum* Ferr. Among those developing on first-instar hosts the females were in the minority to the

extent of 5 : 7, whereas on mature host larvæ they predominated in the ratio of 2 : 1.

Brunson, in the publication already referred to, has given an account of an exceptional variation in the sex ratio induced by a difference in size of hosts. *Tiphia popilliavora* Roh. is a solitary external parasite of the Japanese beetle imported from the Orient some years ago. It normally attacks third-instar hosts, but under field conditions in the United States it emerges and is ready for oviposition so early in the season that very few third-instar grubs are available, the great majority being still in the second instar. Collections of parasitized grubs made during August and held for emergence of the parasite showed a sex ratio of 1 : 93, the males predominating, from small second-instar grubs, 1 : 28 from all second-instar grubs, and 2 : 1, the females predominating, from hosts in the third instar.

More recently (1937) the same author has presented further information on this subject. Eggs deposited on small grubs were transferred to third-instar grubs for hatching and development. Even with the greater amount of food available the sex ratio of the progeny remained virtually identical with that from small grubs. Transfer of eggs from large to small grubs likewise effected no change in the sex ratio. It thus appears that the sex of the progeny is determined by the female at the time of oviposition, a great preponderance of fertilized eggs being placed upon third-instar grubs and of unfertilized eggs upon those of the second instar. These findings corroborate the conclusions reached by Chewyreuv in the case of *Pimpla*.

Another phase of the sex-ratio problem is presented by Flanders (1936) in connection with his studies on aphelinid parasites of scale insects. Certain of these species develop as both primary and secondary parasites and several authors have pointed out that the individuals developing in the latter rôle are invariably males. Flanders now finds that in certain species of *Coccophagus* the males can be produced only hyperparasitically, whereas the progeny from the coccid host are exclusively females. Related to this phenomenon is the fact that the oviposition response of the parent female changes at the time of fertilization. When unmated she is attracted only to previously parasitized scales, and

places her egg only in the body of the primary parasite larva, whereas after mating she oviposits only in unparasitized scales. In those groups in which this relationship is not obligatory the host of the hyperparasitic male, being smaller than the coccid host, may govern the sex of the parasite.

From the data presented it will be seen that the idea of the sex ratio of any given species being even approximately a fixed figure is entirely untenable. It will vary (1) with the sex ratio of the host; (2) with successive generations upon the same or a different host generation; (3) with different hosts; (4) upon the same host and in the same season, but in different geographical regions; and (5) in successive years when the host population is increasing or declining rapidly. Increase in host density is often reflected in a reduction in size of individuals, with a consequent influence on the sex ratio of the parasite. Theoretically the greatest opportunity for a constant sex ratio should be in a monophagous parasite species of solitary habit, such as *Chelonus*, which oviposits in the host egg and develops in the larva, in a host species having a minimum difference in size between the sexes and a single generation each year.

It follows logically that the value of any quoted sex ratio is dependent upon the supporting data accompanying it. This should include the sex ratio of the host generation upon which the parasite developed (applicable when both sexes are attacked), the stage of the host (applicable only when attack is not restricted to a single instar), the locality of collection, and the dates of rearing. When possible, separate figures should be given for those reared from each host sex and for each parasite generation during the season.

The facts presented illustrate quite clearly the great influence which the factor of size of host exerts upon the sex of the parasite that develops upon it. In some cases, though by no means in all, this information can be applied in a practical way in biological control work involving the rearing, in the insectary, of stocks for colonization. A higher ratio of females will permit of a more rapid increase in number of the rearing stock or, conversely, it will permit the production of a given number of females for colonization at a lower cost and with less labor.

Among those monophagous parasites which reveal a change in

sex ratio correlated with host size, advantage should be taken of this opportunity by the use, when possible, of later host instars or, in the case of cocoon parasites, of female cocoons only if there is an appreciable disparity in size between those of the two sexes.

In the case of polyphagous species the opportunity of securing increased production is even greater. Here it is possible not only to utilize the larger individuals of the principal host species, but to make a complete change of hosts for rearing purposes, the species selected being the one of maximum size and greatest availability among the known hosts.

It has been demonstrated in a number of instances that the total number of eggs deposited by females of a given species is in simple proportion to their size. In rearing work the use of large hosts has an added advantage. Not only is the proportion of female progeny higher, but their reproductive capacity is greater, thus permitting a still more rapid build-up of stocks for colonization purposes.

One very important problem in many biological-control projects is the decline in proportion of females in successive generations when reared under insectary conditions. In a number of instances this has led to the final loss of breeding stock. Where this difficulty is encountered particular attention should be given to host size to determine if a selection of host stages or a change of host will lessen or overcome the tendency towards excessive production of male progeny. This tendency apparently is not always due to lack of proper mating.

Another way in which this relation between host size and the sex ratio of parasites can be put to practical use is in the time of colonization of introduced species. Where the parasite normally attacks its host in several larval instars it may prove to be a distinct advantage to make releases when the later instars predominate in the field. With polyphagous parasites the initial liberations might be advantageously made upon a host different from the one for which control is sought.

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